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HELIOTROPIC ANIMALS AS PHOTOMETERS ON THE BASIS OF
THE VALIDITY OF THE BUNSEN-ROSCOE LAW FOR
HELIOTROPIC REACTIONS

By Jacques Loeb and John H. Northrop

ROCKEFELLER INSTITUTE FOR MEDICAL RESEARCH, NEW YORK CITY

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While it was customary to express animal instincts in terms of human behavior, one of us many years ago began to replace this anthropomorphic method by the objective and quantitative methods of the physicist. These methods were most easily applicable in the case of those instincts familiar to every layman in which animals were apparently attracted or repelled by light. Loeb¹ was able to express the effect of light in these cases in the following terms: Certain animals are compelled automatically to orient their body in such a way that symmetrical elements of their photosensitive surface are struck by light of the same intensity. In that case the tension and energy production in the symmetrical muscles of both sides of the body are equal and there is no reason for the animal to deviate from this direction of its motion. If, however, the symmetrical photosensitive elements (e.g., the eyes) receive unequal illumination the tension or energy production of the symmetrical muscles is no longer the same and the animal is automatically turned until its orientation is again such that symmetrical photosensitive elements receive the same amount of light.

It was obvious from the observations that this reaction was a function of the constant intensity of light and Loeb assumed that it was a photochemical effect and that the function was probably the law of Bunsen and Roscoe, whereby the effect equals the product $i t$, where i is the intensity of light and t the duration of illumination.²

The proof for the correctness of this view was furnished for the heliotropic curvatures of the hydroid *Eudendrium* by Loeb and Ewald⁵ and by Loeb and Wasteneys.⁴ The authors could show that if the intensity of light was lowered the time required to call forth the heliotropic curvatures of the polyps had to be increased in such a way as to keep the product $i t$ constant.

A second proof was furnished by Ewald⁵ who showed that when constant illumination was replaced by an intermittent one the same effect could only be produced when the product of time of exposure and intensity of intermittent light was the same as that of a constant light. Ewald worked on the orientation of the eye of *Daphnia* to light. This crustacean turns its eye to the light and when the eye is under the influence of two lights of equal intensity the eye is turned in a direction at right angles to the line connecting the two lights. By keeping the one light constant, the other intermittent (through rotating a disk with a sector cut out in front of it) Ewald found that the two lights acted in an equal way when the product $i t$ in both cases was equal.

The experiments of *Eudendrium* as well as Ewald's experiments are tedious and it seemed desirable to have a simpler method for the verification of this law. Bradley M. Patten⁶ in working on the heliotropic reactions of the larva of the blowfly (which is negatively heliotropic) determined the path of the animals under the influence of two different sources of light striking the animals simultaneously. Theoretically the animal should creep in such a direction that the intensity of illumination on both sides of its photosensitive elements should be equal, and Patten could prove that for each ratio of the two sources the path was a definite one. By rotating a wheel with a sector cut out before one source of light and cutting down the intensity of the other by a slit Patten could also show that indeed the heliotropic effect is determined by the product of intensity into duration of illumination.

"Using the apparatus described, one of the beams of light was cut down by a diaphragm and the other by an episcotister, so that the light coming from one side was a steady beam of low intensity, and that from the opposite side an intermittent beam in which bright flashes alternated with darkness. The apertures in the sector wheel were adjusted so that the amount of light from each source was equal for a unit time. It has already been established that when the larvae are subjected to equal steady beams of light from opposite directions the aggregate response is almost precisely at right angles to the line connecting the sources of light. The average angular deflection of 200 trials at equality was only 0.09° , when the degrees represented a distance of

but 1.5 mm. If the Bunsen-Roscoe law holds for the phototactic response of the larvae, they should orient perpendicularly to the rays of light when subjected to the action of steady and intermittent lights of equal energy per second. The experimental results based on 136 trials made under these conditions show an average angular deflection of but 0.07° from the perpendicular. These results seem to show that in the blowfly larva the phototactic reaction follows the Bunsen-Roscoe energy law.¹⁷

It seemed desirable to extend the proof for Loeb's theory of animal heliotropism and especially for the validity of the Bunsen-Roscoe energy law to other forms of animals, and we selected for the purpose the reactions of the larvae of the barnacle which were already utilized by Groom and Loeb⁸ in their early experiments on the transformation of positively heliotropic animals into negative ones and vice versa.

These larvae move in a straight line towards or away from a single source of light, and when two lights of equal intensity are given they move in a line at right angles to the line connecting the two lights. These animals are small and can be obtained in large numbers. They were made to collect in the corner of a dish with a little sea water and were then sucked up into a pipette which was blackened with the exception of the opening. When such a pipette is put into a glass dish with parallel walls whose bottom is black (by putting paraffin blackened with lamp black at the bottom of the dish) the larvae will flow out in a fine stream and swim when they are positively heliotropic in a straight line towards the source of light. They thus form a rather narrow white trail on the dark bottom and it is possible to measure the angle of this trail with the line connecting the two lights. In this way in each observation the trail of thousands of individuals is measured. By using one constant and one intermittent source of light and comparing the results with those obtained by two constant lights we can test the validity of the Bunsen-Roscoe law.

The method of the experiments was as follows: *a b c d* (fig. 1) is a square dish of optical glass with blackened bottom and containing a layer of sea water. *A* and *B* are two lights, the intensity of which is determined by a Lummer-Brodhun contrast photometer. In front of each light is a screen with a round hole permitting a beam of light to go to the dish. The lights and the dish *a b c d* are so adjusted that the two beams of light striking the sides *a b* and *b c* at right angles cross each other in the middle of the dish. The light *A* is fixed while the light *B* is movable on an optical bench. The experiment is made in a dark room and the lights *A* and *B* are enclosed in a box. At the begin-

ning of the experiments the pipette is filled with a dense suspension of larvae in sea water and then put with its point touching the bottom of the dish. The animals flow out in a fine stream which is narrow at the opening of the pipette and widens slightly, owing probably to the negative stereotropism of the animals. A glass plate (fig. 2) *h i k l*, which has a strong red line *n o* and a fine parallel line *p g* (cut with a diamond), is then put on the dish and so adjusted that *p g* is in the middle of the stream *f g* of the animals. Then the angle α which *p g* makes with the perpendicular from *A* on *a b* is measured. This per-

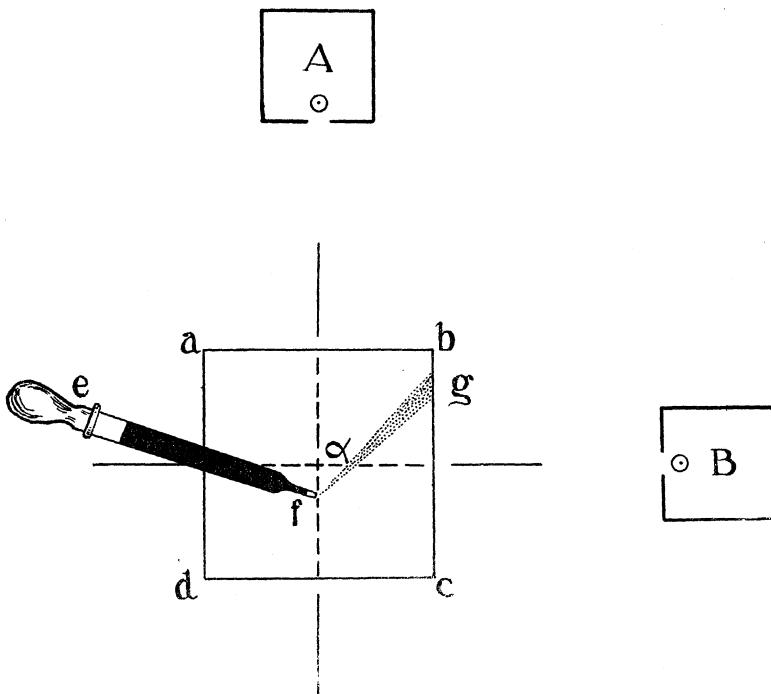


FIG. 1.

pendicular is marked in the form of a red line on the black base on which the glass vessel *a b c d* stands. The angle α is measured with a goniometer. When the lights are equal in intensity α should be 45° ; if the two lights have different intensities and if *A* be the stronger light α should become smaller with increasing difference in intensity. The individual measurements vary comparatively little, as long as the difference in the intensity of the two lights is not too great; for this reason our observations do not go beyond a wider ratio of the two lights than 10:1. Table 1 gives the results. *A* is always the stronger light.

Each table is the average of from 40 to 60 individual observations, each being the average of the path of many thousands of animals.

In the next series of experiments an opaque rotating disk with one sector cut out was placed before light *B*. In one set of experiments the sector cut out was 90° . The rate of rotation (by an electric motor) was 1,500 to 2,500 revolutions per minute. The other light was constant and its position was chosen on the assumption of the validity of the Bunsen-Roscoe law for these cases. Thus when the two lights without sector were equal at a given distance of *A*, by putting the 90° sector before *B*, it was assumed that the ratio of effects would be the same as if, with constant light, *B* had been placed at the double distance and the ratio of intensities of the two lights had been 4:1. Going on such a calculation we should expect the same values for α as in table 1.

As one sees the observed values are slightly smaller but practically identical with the values obtained when the two lights are constant. The deviation is probably due to the fact that the photochemical efficiency of an intermittent light is a trifle less than that calculated on the basis of the Bunsen-Roscoe law.⁹

We carried out some experiments with a sector of 144° . When the efficiency of both lights was equal on the assumption of the validity of the Bunsen-Roscoe law α was found to be 44.9° (instead of 45°), and for the ratio 2:1 α was found to be 38.8° . The values are, within the limits of error, identical with the values in tables 1 and 2.

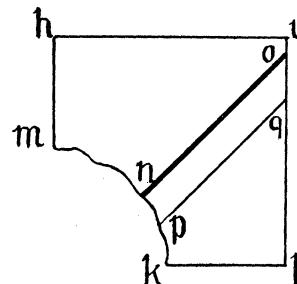


FIG. 2.

TABLE 1

	VALUE OF α FOR DIFFERENT RATIOS OF INTENSITIES OF THE TWO LIGHTS			
Ratio of the two lights.....	1:1	2:1	4:1	10:1
Value of α (direction of path).....	45.6°	40°	34.4°	28.8°

TABLE 2

	VALUE OF α WHEN ONE LIGHT IS INTERMITTENT (90° SECTOR) AND THE OTHER CONSTANT AND THE EFFICIENCY OF THE TWO LIGHTS IS CALCULATED ON THE BASIS OF THE VALIDITY OF THE BUNSEN-ROSCOE PHOTOCHEMICAL LAW		
Ration of the two lights.....	1:1	2:1	4:1
Value of α	44.2°	38.3°	34.1°

Summary.—The paper gives some new quantitative experiments proving that the ‘instinctive’ motions of animals to light are phenomena of automatic orientation (heliotropism) and a function of the constant intensity of light; the exact expression of the function being the Bunsen-Roscoe law of photochemical action.

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³ Loeb, J., and Ewald, W. F., *Zentrabl. Physiol.*, Wien., 17, 1914, (1165).

⁴ Loeb, J., and Wasteneys, H., *J. Exp. Zool., Wistar Inst., Philadelphia*, 22, 1917, (187).

⁵ Ewald, W. F., *Science, New York*, 38, 1913, (236).

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⁹ Parker, G. H., and Patten, B. M., *Amer. J. Physiol.*, 31, 1912-13, (22); Abney, W. de W., *Report 59th Meeting, British Assoc. Adv. Sc.*, 1899, (481); *Treatise on photography*, 10th ed. London, 1907; Englisch, E., *Arch. wiss. Phot., Halle*, 1, 1899, (117).

THE APPEARANCE OF REVERSE MUTATIONS IN THE BAR-EYED RACE OF *DROSOPHILA* UNDER EXPERIMENTAL CONTROL

By H. G. May

DEPARTMENT OF ZOOLOGY, UNIVERSITY OF ILLINOIS

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During some experiments in selection for higher and lower facet numbers in the bar-eyed race of *Drosophila ampelophila* I obtained six full-eyed males and five heterozygous females from the stock bottles and the selected lines.

In appearance these flies could not be distinguished from normal full-eyed males and heterozygous females. Three males and three females were mated with bar-eyed flies and gave the offspring anticipated from such normal flies. In two cases the males gave only bar-eyed male offspring and heterozygous female offspring. In the third case the offspring were not examined until twenty-four days after the mating had been made and as the result of the hatching of individuals from the second generation bar-eyed females and full-eyed males were also present. The offspring of the heterozygous females in each case consisted of bar-eyed and full-eyed males and bar-eyed and heterozygous females. Some of the offspring of a full-eyed male were interbred and produced full-eyed males and bar-eyed females as well as bar-eyed males